SOME ASPECTS OF THE KINETICS IN THE JAWS OF BIRDS

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KINETICS in birds' jaws, as used here, means a dorsoventral motion of the rostral portion of the skull on the cranial part of the skull. Where these two parts come together there is a frontonasal "hinge." The hinge is a horizontal bony plate variously composed of thin extensions of the nasal, premaxillary and frontal bones. Although there is definite articulation here in some species (parrots, for example), in most the movement is partly, if not entirely, made possible by the flexible nature of the thin bones in this region (Figs. 1, 2, 3).

Since the maxillary bones are firmly fused to the nasals in birds, the maxillary must move if the nasal bone moves. When the maxillaries move, the palatines, pterygoids and quadrates also move. As a matter of fact, the chain of sequence is in the opposite direction. Forces applied by muscles to the pterygoids and quadrates cause these bones to move, and their movement impinges on the next bone. The end result is, as we have said, a dorsoventral movement of the upper bill in birds.

Thus, the visible "jaw kinetics" in birds is but a part of the entire mechanism. Kinetics in the classical sense of comparative anatomy encompasses a much wider area including jaw suspension. Type of jaw suspension and kinetics have long been thought to vary with food habits. Differing food habits are also believed to be important selective devices in the evolution of animals. Thus the kinetics of jaws may be a fruitful field for the study of significant adaptations.

Most of the structural parts of the kinetic avian jaw have been known for some time (Nitzsch, 1816; and Huxley, 1867). The basic pattern of bone, muscle, and ligament is well established in the literature (Hofer, 1945, 1950; and Fiedler, 1951). However, it is the change from a basic pattern that is of primary interest to one attempting to correlate food habits with the details of structure and function. In recent years, workers (Kripp, 1933-1935; Engels, 1940; Beecher, 1950-1951) have emphasized the structural differences found upon dissection and have tried to correlate these with food habits. Observing the details of function in a living bird seems beyond the realm of possibility at present.

We must then try to visualize the functional aspect from the structural plan. This is a procedure fraught with the dangers of misinterpretation of the actions and co-actions of the many parts of the kinetic mechanism. Nevertheless, if we are to study this morphogenetic area or apparatus of the bird, we must do the best we can. All qualitative features must be known

and we must emphasize the quantitative nature of the mechanism. Subjective evaluations of quantitative materials are notoriously poor. Weight, volume and length of muscles, angle between muscle and bone, relative vectors of muscular force, length of work and force arms on the bony levers, and total movement of the upper bill are but a few of the features that should actually be measured. Knowing these, one can set up physical formulae to calculate the relative effectiveness of the varying jaw apparatuses found in birds.

Kripp (1933-1935) was one of the first to emphasize the functional view, but his complex lever systems fail to include the varying muscular forces that might be indicated, in a relative way, by weights or volumes. Barnikol (1951) studied the problem more recently on a qualitative basis. The only study, of which I am aware, that includes most of the variables known is Donald C. Goodman's (1954) unpublished analysis of the functional features of the kinetic apparatus in waterfowl.

Fisher and Goodman (1955) devised a reliable method of measuring the total movement at the frontonasal hinge.

This present study is designed to demonstrate some of the factors which affect the dorsoventral movement at the hinge between the rostral and cranial parts of the skull. It is by no means an exhaustive work. Rather, it is hoped that the paper will stimulate others to undertake the detailed and extensive studies that will be necessary.

MATERIALS

It is the custom of many hunters of waterfowl at the Horseshoe Lake Refuge in Illinois to have their game cleaned and dressed by professionals. I obtained 75 heads of Canada Geese (*Branta canadensis interior*) and 23 heads of Mallard Ducks (*Anas platyrhynchos*) from these cleaners. Most of the kill was made before noon, and the heads were received shortly after noon. Thus the specimens were as nearly fresh as possible. One group of 20 goose heads was not measured until 24 hours after death.

The 17 American Crows (*Corvus brachyrhynchos*) used in this study were collected at Fairmount Quarries in Vermilion County, Illinois. All measurements on the fresh heads were made within eight hours after collection.

The Double-crested Cormorants (*Phalacrocorax auritus*) were taken from a single breeding colony at Spring Lake, Carroll County, Illinois.

At the Camp Creek Duck Farm at Monticello, Illinois, Pekin Ducks are dressed for market in the morning. We measured the kinetics in these young ducks in the afternoon of the day they were killed. A total of 103 heads of Pekin Ducks was provided by this farm.

Opportunism is evident in the list of materials. It is apparent that the specimens were not selected to show a wide variety of either taxonomic types or of food habits. To secure sufficient numbers of specimens for statistical analysis, it was necessary to choose species easily obtained.

The skulls are preserved in the Natural History Museum of the University of Illinois.

The Experiments

Preliminary dissections indicated that bony parts, ligaments and the muscles themselves might be factors restricting the amount of movement — either protraction or retraction. Method of preservation of the head, method of preparing the skeleton, and, when dealing with fresh materials, the length of time between death and the measurement were believed to be other factors affecting the apparent movement.

Experiments were designed to evaluate the:

1. Consistency in the results of measurement of skeletal specimens. Consistency might indicate the presence of a bony structure that finally stopped the movement, before actual fracture of the delicate hinge.
2. Limitations imposed by the bulk of the muscle mass, no matter whether these muscles were part of the kinetic mechanism or not.
3. Limitations resulting from the presence of ligaments, joint capsules, and strong fascia (see Fig. 4).
4. Validity of the use of museum skulls as an indication of the degree of kinetics in fresh specimens. It is necessary to soak or steam a skull before the kinetics can be measured. The length of time and the temperature of the water may affect the movement.
5. Validity of the use of preserved materials as an index to the kinetic condition.
6. Effect of the use of preserved specimens as an index to movement.

In all the following experiments, measurements of kinetics were made

with the machine described by Fisher and Goodman (1955). Museum skulls were soaked in water of different temperatures. At least 24 hours elapsed between the successive measurements of skulls that had to be soaked more than once. Unless stated otherwise, skulls were uniformly soaked for one hour in water that was at 100 degrees F. when the skulls were placed in it.

Preserved materials were kept in a mixture of one gallon of 10 per cent formalin and one pint of glycerin. Before preservation, all muscles were removed from the head. Before measuring, the heads were soaked in cold water.

In all instances within a species the same heads were used for a complete experiment. Thus in Table 4, the same 52 heads of Canada Geese were measured when they were fresh and complete, fresh with muscles removed, fresh with muscles removed and ligaments cut, and when prepared as museum skulls. A different series of 20 heads was measured when fresh and when preserved. Changes indicated are ones that actually occurred and are not just what might be found by measuring two different series under the conditions stipulated.

Discussion of the Data

If the bony construction of the skull includes a "stop" for kinetic movement, measurements of museum skulls should produce consistent and reliable data. The data on a series of 30 cormorant skulls are presented in Table 1. Variation between the findings of two different observers indicates that no mechanical stop, other than perhaps the rigidity of the hinge, is operating. The significant difference results from different pressures applied by the observers.

Table 1
Degrees of Movement of the Fronto-nasal Hinge in Double-crested Cormorants

	No. specimens	Mean	Standard deviation	Range	Coeff. variation	
Observer 1	30	20.8±0.29	1.59	18–24	7.6	highly signifi- cantly
Observer 2	29	30.7±0.52	2.80	25–35	9.1	different

However, in the crow there is a definite bony stop. The orbital process of the quadrate has an enlarged, clapper-like end which presses against a papilla in the posteroventral part of the orbit (Fig. 1) when protraction (dorsal movement of the upper bill) is greatest. This may be observed in fresh heads. Table 2 shows relatively close agreement between the degrees of movement in fresh heads and in museum skulls of crows. It may be observed in Table 3 that in all the species studied there is a significant

change in apparent degrees of movement when fresh heads are prepared as museum skulls. Further, the coefficients of variation are greater for skull measurements than for any other measurements. These observations indicate that protraction in living birds may be halted by factors other than bony structures. Even in the crow, the special structure is at most a "final stop" as shown by the fact that fresh heads have a significantly smaller amount of movement.
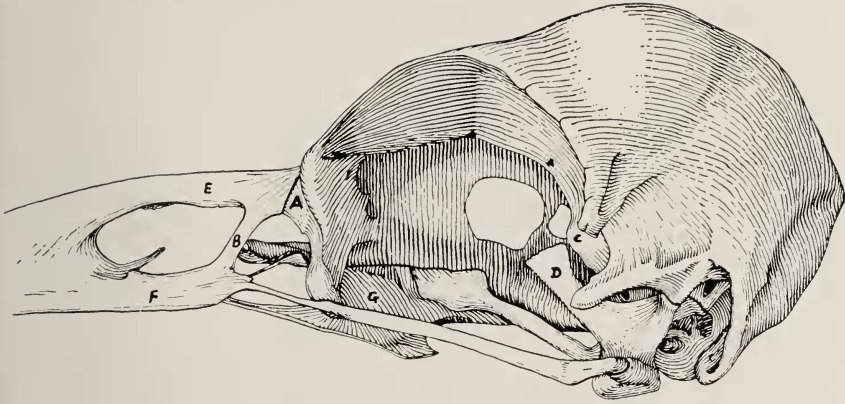

Fig. 1. Lateral view of the skull of an American Crow. A is the lacrimal bone ("retractor stop"); B, the nasal process of the maxillary; C, the "protractor stop" on the posterior wall of the orbit; D, the orbital process of the quadrate; E, the nasal bone; F, the maxillary bone; and G, the palatine bone.

TABLE 2

DEGREES OF MOVEMENT OF THE FRONTO-NASAL HINGE IN SEVENTEEN CROWS

	Mean	Standard deviation	Range	Coeff. variation	
Fresh heads: complete	16.9±0.38	1.57	14–19	9.3	
Museum skulls: soaked 1 hr. at 100° F.	19.0±0.62	2.57	14–24	13.5	increase 12.4%; P<.01
soaked 3 hrs. at 100° F.	20.1±0.76	3.12	10–26	15.5	increase over 1 hr. soaking 5.8%; P>.10
soaked 30 min. at 180° F.	21.2±0.75	3.09	12-29	14.7	increase over 1 hr. soaking 11.6%; P=.05

Bony structures that stop retraction seem to be more plentiful. This might be expected, for the upper bill is usually in the retracted position and maintenance of this position might cause considerable strain on the relatively small retractor muscles. With the several bony stops described below there is no muscular effort necessary, once the bill is retracted.

In the Canada Goose there may be found on the anterior tip of the base

Fɪɢ. 2. Lateral view of the area of the frontonasal hinge in *Balearica* to show the ("retractor stop").

of the lacrimal a tooth-like projection which fits into a notch in the postero-dorsal part of the nasal process when the bill is retracted (Fig. 3 B). The fit between the "tooth" and the notch is close when the bill is fully retracted. Further, abnormal retraction results in a pull against the length of the bones in the hinge. Without the tooth and notch, abnormal retraction would cause a transverse, breaking force against the bones. The difference is important, because bones may withstand much more force exerted along their long axes than at right angles to these axes. Similar stops are present in the Lesser Scaup (*Aythya affinis*), Mallard (*Anas platyrhynchos*), Whistling Swan (*Cygnus columbianus*), and Hooded Merganser (*Lophodytes cucullatus*). It is not well developed in the latter.

In the cranes *Balearica* (Figs. 2, 3C), *Grus*, and *Anthropoides*, and in the Domestic Pigeon (*Columba livia*) a somewhat different retractor stop is found. In these birds the thin nasal process extending dorsoposteriorly to the hinge comes to rest on the dorsointernal edge of the lacrimal when retraction is complete. In *Corvus* (Fig. 1) the nasal process comes to rest partly on the anterodorsal corner of the lacrimal but primarily on the dorsal end of a much inflated bone closely applied to the anterior surface of the lacrimal.

Another source of variation in the measurement of kinetics in museum skulls may be found in the greater flexibility of skulls of young birds. Even casual study of skulls reveals the lesser ossification of the hinge in young birds. The Pekin Ducks may be used as an example. The series for which data are presented in Table 6 was composed of young ducks, because those were the ones primarily available. Five adults were measured; fresh, they averaged 24.6 degrees of movement; as skulls, the movement was 28.0 degrees. If these are compared to data in Table 6, it is seen that the measure-
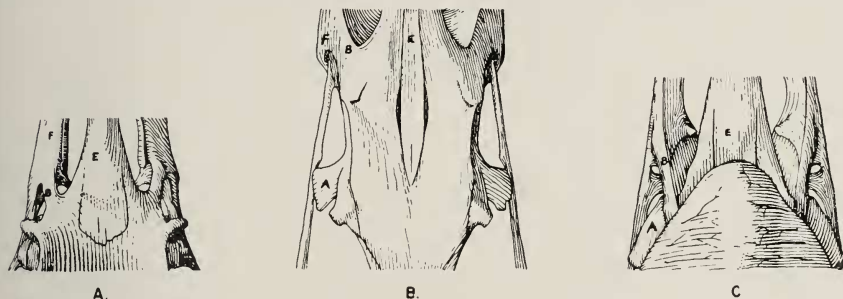

Fig. 3. Dorsal views of the area of the frontonasal hinge in *Corvus* (A), *Branta* (B), and *Balearica* (C). See legend for Fig. 1.

ments of fresh specimens corresponded fairly closely to those of young ducks, but the measurements on skulls were lower.

Related to this variation is another which concerns the preparation of skulls. In Tables 4, 5, and 6 it is apparent that readings for museum skulls were always lower than for the same skulls when they were fresh but had all the muscles and ligaments removed. At first thought this does not seem logical; the only difference is the drying, "bugging," bleaching and/or degreasing to which the museum skulls have been subjected. However, it is apparent that these processes reduce the possible movement, either by affecting the articulations or the flexibility of the bones themselves. The effect may be brought about by removal of the organic materials.

It is of passing interest that mean movement as measured on skulls in

TABLE 3

INCREASES IN DEGREES OF MOVEMENT OF THE FRONTO-NASAL HINGE WHEN FRESH HEADS ARE PREPARED AS MUSEUM SKULLS

Canada Goose	4.3 degrees (19.4%)	$P < .01$
Mallard Duck	10.5 degrees (44.8%)	$P < .01$
Pekin Duck	7.8 degrees (31.2%)	$P < .01$
American Crow	2.1 degrees (12.4%)	$P < .01$

no instance showed a significant variation from mean movement as indicated by measurement of fresh heads from which the muscles had been removed (Tables 4, 5, and 6).

Since skulls must be soaked prior to measurement, the soaking may introduce other errors. Table 2 contains data from a few experiments on this factor. It seems evident that skulls must be soaked a uniform length of time for measurements to be accurate and comparable.

The experiments with Canada Geese (Table 4), Mallard Ducks (Table 5) and Pekin Ducks (Table 6) demonstrate a significant change when all the muscles are removed. The increase varies from 14 per cent in the Canada Goose to 49 per cent in the Mallard. One might expect some change as the result of removal of the retractor muscles which oppose protraction. But this seems to be something more. In a few fresh specimens all cranial muscles having a possible retractor function were cut across. The amount of movement did not increase significantly over that found in fresh, complete heads. It is thought that simply the bulk of the muscles is a limiting factor.

One might also believe, since the ligaments were still intact, that the limitations imposed by the ligaments prevented a clear-cut demonstration of muscular limitation. However, Tables 4, 5 and 6 contain data which show a significant change when all the ligaments are cut on these same heads. This increase over the movement found when just the muscles were removed ranges from 16 per cent in the Mallard to 28 and 33 per cent in the two series of Pekin Ducks.

There are perhaps eight or ten ligaments which may limit the movement. The diagram (Fig. 4) shows the position of some of these. In addition to these ligaments, the connective tissue in the ligamentous capsules surrounding the joints may be a limiting factor. It was not possible to test for the effectiveness of each individual ligament and joint capsule.

It seemed, from observations made during the measurement of heads in various stages of removal of parts, that the lacrimo-maxillary "ligament" (a broad band of fascia), the pterygo-palato-orbital ligament, and the vomero-orbital ligament were the most important limiting ligaments. Attention was centered on these and on the capsule about the articulation between the pterygoid bone and the basipterygoid process (Fig. 4).

A second series of Pekin Ducks (Table 6) was used to test the effects of successive removals of various ligaments. Data in this table indicate that removal of all ligaments shown on the diagram (Fig. 4) except the lacrimo-maxillary, pterygo-palato-orbital, and the vomero-orbital resulted in an increase of 5.2 degrees of movement (15.8 per cent).

When the lacrimo-maxillary ligament or fascia was cut, no demonstrable

TABLE 4   Degrees of Movement of the Fronto-nasal Hinge in Canada Geese

	No. specimens	Mean	Standard deviation	Range	Coeff. variation	Percentage change	Probable significance of change
Fresh heads: complete	52	22.2±0.26	1.86	17-26	8.4		
all muscles removed	52	25.3±0.32	2.34	19-32	9.2	increase 14.0	P<.01
all ligaments cut	52	30.3±0.36	2.59	20-38	8.5	increase 19.8	P<.01
Skulls: museum preparation	51	26.5±0.44	3.16	17-34	11.9	decrease 12.5	P<.01
Fresh heads: complete (within 8 hrs. of death)	20	21.6±0.45	2.03	18-29	9.4		
Preserved heads: muscles removed; ligaments intact	20	18.7±0.46	2.07	14-23	11.1	decrease 13.4	P<.01
Fresh heads: complete (about 24 hrs. after death)	20	20.8±0.47	2.10	20-32	10.0		

TABLE 5   Degrees of Movement of the Fronto-nasal Hinge in Mallard Ducks

	No. specimens	Mean	Standard deviation	Range	Coeff. variation	Percentage change	Probable significance of change
Fresh heads: complete	23	23.4±0.59	2.84	18-30	12.1		
all muscles removed	23	34.9±0.66	3.15	28-42	9.0	increase 49.1	P<.01
all ligaments cut	23	40.3±0.58	2.77	33-48	6.9	increase 15.5	P<.01
Skulls: Museum preparation	21	33.9±0.71	3.20	23-40	9.4	decrease 15.9	P<.01

change occurred although tightening of this ligament may be seen when the bill is protracted by one's hand.

Removal of the capsule around the pterygoid-basipterygoid articulation increased the movement by 1.8 degrees (P>.10).

When the pterygo-palato-orbital and vomero-orbital ligaments were removed from the same specimens, the movement increased significantly by 3.8 degrees or 9.5 per cent.

PTERYGO-PALATO-ORBITAL LIGAMENT
VOMERO-ORBITAL LIGAMENT
LACRIMO-MAXILLARY "FASCIA"
LACRIMO-JUGAL LIGAMENT   JOINT CAPSULE
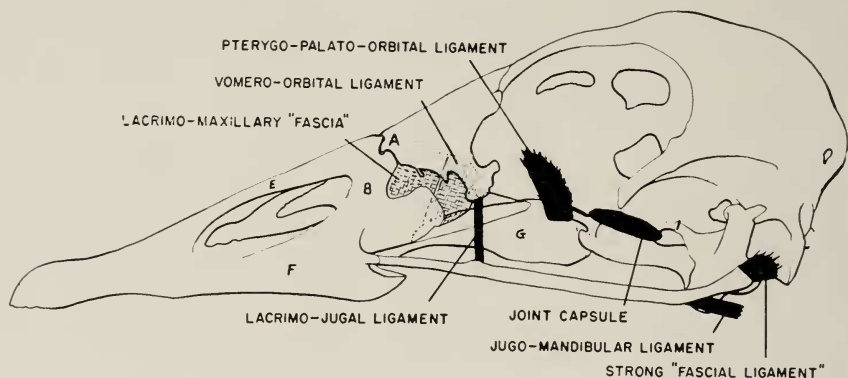JUGO-MANDIBULAR LIGAMENT
STRONG "FASCIAL LIGAMENT"

Fig. 4. Lateral view of the skull of a Canada Goose, showing the positions of some soft structures which limit kinetic movement.

The increases noted above, whether they were in absolute or percentage values, can not be construed as the actual extent of limitation caused by the parts removed. The sequence of removal undoubtedly plays a major role in determining these values. Had it been feasible to remove the muscles, ligaments and capsules in different sequences, the values might well have been different. What these increased movements do show is that all these structures are parts of the total mechanism that limits protraction.

The Criteria for Reliable Measurement of Avian Jaw Kinetics

Knowing that all these soft and bony structures may restrict protraction, or retraction, it is obvious that no valid conclusions concerning the amount of movement can be based solely on measurements of museum skulls. Unless one has previously established for a species an index of relationship between measurements of fresh heads and of skulls, skulls cannot be used. (Note the variations between the species of waterfowl in Table 3 and variation with museum preparation, soaking, and age.)

Preservation of heads in formalin and glycerin and the subsequent soaking that is necessary prior to measurement reduce significantly the amount of movement (Table 4).

TABLE 6   DEGREES OF MOVEMENT OF THE FRONTO-NASAL HINGE IN YOUNG PEKIN DUCKS

	No. specimens	Mean	Standard deviation	Range	Coeff. variation	Percentage change	Probable significance of change
Fresh heads: complete	83	27.0 ± 0.40	3.64	19-38	13.5		
all muscles removed	44	32.4 ± 0.63	4.17	23-42	12.9	increase 20.0	P < .01
all ligaments cut	43	41.5 ± 0.78	5.10	26-55	12.3	increase 28.1	P < .01
Skulls: museum preparation	20	33.0 ± 1.33	5.97	21-48	18.1	decrease 20.5	P < .01
Fresh heads: complete	19	25.0 ± 0.45	1.96	21-30	7.8		
all muscles removed	19	32.9 ± 0.72	3.13	29-40	9.5	increase 31.6	P < .01
only lacrymo-maxillary, pterygo-palato-orbital, and vomero-orbital ligs. remain	19	38.1 ± 0.73	3.20	30-45	8.4	increase 15.8	P < .01
lacrimo-maxillary ligament cut	17	38.0 ± 1.03	4.26	30-46	11.2	no change	
pterygo-basipterygoid capsule removed	17	39.8 ± 1.18	4.86	29-55	12.2	increase 4.7	P > .10
pterygo-palato-orbital and vomero-orbital ligs. cut	19	43.6 ± 0.77	3.34	36-52	7.7	increase 9.5	P = .01
Skulls: museum preparation	19	32.8 ± 1.23	5.36	22-42	16.3	decrease 24.7	P < .01

Fresh heads are thus the only satisfactory material for measurement of kinetics in birds. It is not always possible to obtain and measure these heads immediately after death. With the exception of a series of 20 Canada Geese, all fresh heads in this study were measured within eight hours of death. Coefficients of variation of these were not unduly high; they were no higher than the coefficient of variation for the series of Pekin Ducks which had just been killed. Amount of movement in the 20 geese that were measured 24 hours after death was not significantly different from that found in another series of 20 measured within eight hours of death. The only special treatment the "24-hour" skulls received was that they were refrigerated and that the stiffness was removed by protracting the bill several times before the measurements were made.

Series must have an adequate number of specimens in them. If one looks over the data presented in the tables, it becomes apparent that there is con- siderable variation of several kinds. Therefore, we can not study kinetics from measurements or dissections of one or a few specimens. Even with samples of 83 and 19 in Table 6 note that there is an apparently significant difference (27.0 ± 0.40 versus 25.0 ± 0.45) between the two series of fresh heads of Pekin Ducks!

Summary

The kinetics of the avian skull, defined as protraction and retraction of the upper bill, can be a source of valuable information on the evolution of the feeding mechanism and consequently on the evolution of the species. But accurate and consistent quantitative studies of kinetics must be made before conclusions are drawn.

This study has contributed the following information pertinent to the gathering of quantitative information and to the limitations on movement:

1. As just noted, there must be a sufficient number of specimens in a series for the results to have some statistical reliability.

2. Intact, fresh heads must be used; they may be measured as long as 24 hours after death.

3. Skulls prepared for museum collections do not permit reliable or consistent measurement; soaking, "bugging" or cooking, degreasing and bleaching these skulls give rise to great variability in kinetic movement.

4. Skulls may not even be used as an index to kinetics unless there has been established for a species a definite relationship between measurements on the skull and measurements on the complete, fresh head.

5. Heads preserved in formalin and glycerin show a decreased kinetic

movement which makes measurements of them incomparable with measurements of other materials.

6. Although some species, such as the American Crow, possess definite bony structures which stop protraction, most limitation is imposed by soft parts of the head. Retractor stops of bone are present in many species.

7. The entire mass of cranial muscles, including muscles not apparently connected with protraction or retraction, restrains movement.

8. Ligaments, as might be expected, are of major importance in circumscribing kinetic motion. The limitations set up by the vomero-orbital and pterygo-palato-orbital ligaments are noted.

9. Even joint capsules, particularly the one around the articulation between the pterygoid and the basipterygoid process, reduce and limit kinetic activity. The effect of this one capsule was measured.

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